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Phylogenetic analysis of the myrmecophilous *Cremastocheilus* Knoch (Coleoptera, Scarabaeidae, Cetoniinae), based on external adult morphology

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Abstract

The genus *Cremastocheilus* (Coleoptera: Scarabaeidae: Cetoniinae) is a myrmecophilous group of approximately 45 species distributed throughout North America. Authors previously recognized anywhere between two and five subgenera. We present the first cladistic analysis of *Cremastocheilus* based on 51 external adult morphological characters. The monophyly of the subgenera *Macropodina*, *Trinodia* and *Cremastocheilus* is supported. *Cremastocheilus* (*Anatrinodia*) *wheeleri* is most closely related to other *C.* (*Cremastocheilus*). The three species groups comprising *C.* (*Myrmecotonus*) are paraphyletic with respect to *C.* (*Cremastocheilus*). The pronotum, which bears most of the glands that enable beetles to interact with ants, provides important characters, while characters associated with setae and tomenta are homoplastic. Based on examination of the strict consensus of 24 equally parsimonious trees *C.* (*Myrmecotonus*) and *C.* (*Anatrinodia*) are synonymized with *C.* (*Cremastocheilus*).

Keywords

Scarabaeidae, *Cremastocheilus*, phylogeny, myrmecophily

Introduction

Cremastocheilus Knoch is a unique scarab genus that can be recognized by a suite of characters related to its myrmecophilous habit. It can be distinguished from other

genera by distinct anterior and posterior pronotal projections or "angles" that bear exocrine glands and associated trichomes (clumps of setae typically associated with glands). The pronotal angles are highly variable within the genus, particularly in *C. tibialis* which lacks posterior pronotal trichomes entirely. Similarly, posterior pronotal trichomes are found in the New World related genus *Centrochilus* Krikken (see Krikken 1976) as well as Old World genera *Aspilus* Shaum and *Lecanoderus* Kolbe, although none of these genera have modified anterior pronotal angles or associated trichomes (Krikken 1982). In comparison to related genera *Cremastocheilus* is one of the more speciose and probably best studied groups within the tribe Cremastocheilini (Krikken 1984), which includes 51 genera worldwide (Krikken 1984) and ten in the New World, including *Cremastocheilus*. There are approximately 45 recognized species, including several subspecies found throughout North America. As adults, all species are presumed predaceous on ant larvae and, in some cases, pupae, based on collection records and behavioral studies on certain species (see Cazier and Mortenson 1965). Related beetles are also known to be predaceous on other insects, *e.g. Pseudospilophorus plagosus* Boheman preys on soft scale insects in southern Africa (Buttiker 1955), and *Spilophorus maculatus* (Gory and Percheron) from southern India has been documented feeding on membracids (Ghorpade 1975). It is presumed that related species in the tribe Cremastocheilini are also predaceous based on the expanded mentum (Krikken 1984). In addition, no genus, except *Centrochilus* and Old World genera *Aspilus* and *Lecanoderus* bear trichomes like those of *Cremastocheilus*; however, the presence of associated glands makes Cremastocheilus a distinctive genus within the tribe as well as the scarab subfamily Cetoniinae.

Horn (1879) was the first to suggest that trichomes in *Cremastocheilus* species are associated with glands that secrete substances somehow pleasing to ants. In contrast, Wheeler (1908) proposed that pronotal glands emit substances that are irritants that "distract" ants from attacking more vulnerable organs. Others have proposed that trichomes allow the beetles to gain access to ant nests by rapid diffusion of aromatic substances that would allow beetles to be carried into ant nests as food (Cazier and Mortenson 1965). In support of Wheeler, Alpert (1994) recently found that ants "lick" the pronotal glands and are subsequently ignored within the brood chambers, while feeding uninterruptedly on ant larvae. Given the above scenarios it is possible that different *Cremastocheilus* species use various means to gain access to ant mounds or be expelled from them. Alpert (1994) has shown that exocrine glands and their associated trichomes vary greatly among species. In addition, he found that clusters of glandular cells are often located underneath or close to external patches of hair called tomenta, particularly in the abdomens of several species. The frontal tomenta which largely distinguish the subgenus *C.* (*Trinodia*) also indicate closeness with glands inside the head of these beetles, but there is no evidence that pores or other secretive structures are associated with these patches of hair. Alpert's (1994) definitions of various species groups suggested that ant host, habitat, and position of glands and trichomes are good indicators of relatedness or similarity among different species.

In Horn's (1879) revision of *Cremastocheilus* the mentum was used to distinguish between 17 species known at the time. Mann (1914) created a new subgenus named *Myrmecotonus* that would divide *Cremastocheilus* into two groups based on geographic range and emarginated mentum (Table 1). Typical *Cremastocheilus* species bear a mentum that is notched at the base and are distributed throughout the eastern United States. All other known species are distributed throughout the western United States and northern Mexico, and lack a notched mentum. Mann also suggested that an unusual species described by LeConte as *C. wheeleri* would belong to *C.* (*Myrmecotonus*) given the angulate, non-emarginate mentum. Noting the variability of mentum, pronotal, and leg structure within the group, Casey (1915) later described 15 new species and two new subspecies. He proposed two new genera including *Macropodina,* which was named for distinctive enlarged fore tarsi, and *Trinodia*, which included specimens with a distinctive tri-lobed pronotum. Casey also rejected Mann's (1914) subgenus *Myrmecotonus*, noting that most species bear a non-emarginate mentum, which would put all atypical *Cremastocheilus* species and other genera in the subgenus. The subgenus *Myrmecotonus* has been problematic, due to what most authors would admit is a lack of synapomorphies or good subgeneric definition. In contrast with Mann's (1914) suggestion it was treated as a synonym of *C.* (*Cremastocheilus*) by Krikken (1982), and was later recognized by other authors as an ill-defined subgenus (Howden 1971). Alpert (1994) reinstated *C.* (*Myrmecotonus*) due to geographic range.

Casey (1915) also suggested the recognition of one new monotypic subgenus *Anatrinodia* for *C. wheeleri*, based on a transverse, lobiform mentum, but still related to other typical *Trinodia* by possessing a somewhat similar tri-lobed pronotum. Later, Cazier (1938) synonymized the genus *Macropodina* with the genus *Cremastocheilus* based on what he believed to be few supportive characters for generic status. Cazier also synonymized.

Table 1. History of major subgeneric changes in the genus *Cremastocheilus*. Indented names indicate subgenera that are included in the given genus.

Horn 1879	**Mann 1914**	**Casey 1915**	**Cazier 1938**	**Potts 1945**
Cremastocheilus	*Cremastocheilus*	*Cremastocheilus*	*Cremastocheilus*	*Cremastocheilus*
	Cremastocheilus	*Macropodina*	*Crematocheilus*	*Cremastocheilus*
	*Myrmecotonus**	*Trinodia*	*Macropodina*	*Macropodina*
		Anatrinodia	*Trinodia*	*Trinodia*
			Anatrinodia	*Anatrinodia*
Howden 1971	**Krikken 1982**	**Alpert 1994**	**Mynhardt and Wenzel 2010**	
Cremastocheilus	*Cremastocheilus*	*Cremastocheilus*	*Cremastocheilus*	
*Cremastocheilus**	*Cremastocheilus*	*Cremastocheilus*	*Cremastocheilus**	
Macropodina	*Macropodina*	*Macropodina*	*Macropodina*	
	Trinodia	*Trinodia*	*Trinodia*	
	Anatrinodia	*Anatrinodia*		
		Myrmecotonus		

* Indicates inclusion of *C. wheeleri*

Trinodia and the subgenus *Anatrinodia* with *Cremastocheilus* and suggested that *C. wheeleri* is an intermediate form between *C.* (*Trinodia*) and *C.* (*Cremastocheilus*). Similar to Cazier, Potts (1945) only recognized *Macropodina* and *Cremastocheilus* as well defined subgenera, and united *Anatrinodia* and *Trinodia* informally into what he called a single "Trinodia group" in *Cremastocheilus*, following Cazier's (1938) suggestion. Howden (1971) also did not recognize *C.* (*Anatrinodia*) but provided no information on the placement of *C. wheeleri*. It is assumed that Howden's key would place *C. wheeleri* in *C.* (*Cremastocheilus*). Krikken (1982) later reinstated *Anatrinodia* as a unique subgenus due to its unique pronotum and mentum. Recently, Alpert (1994) recognized all subgenera, including *C. (Myrmecotonus*) and *C.* (*Anatrinodia*) based on differences in geographic range previously recognized by Mann (1914).

The aim of this study is to test the monophyly of currently recognized *Cremastocheilus* subgenera and species groups suggested formally by Alpert (1994), and to determine evolutionary relationships among subgenera. We also aim to elucidate the importance of characters for future phylogenetic analysis, with particular focus on characters related to a myrmecophilous habit.

Methods

A total of 450 *Cremastocheilus* specimens were borrowed from The Ohio State University Insect Collection, University of California-Riverside Entomology Research Museum, University of Nebraska State Museum, Los Angeles County Museum of Natural History, Albert J. Cook Arthropod Research Collection at Michigan State University, and the Museo de Zoologia, Universidade de Sao Paolo. Three species, including *C. robinsoni* Cazier, *C. academicus* Krikken, *C. setosifrons* and *C. chapini* Cazier were not included in the analysis due to unavailability of specimens. The inclusion of *C.* (*Macropodina*) *depressus* in the analysis follows Warner (unpublished thesis) who recognized it as a unique species, although previous authors have synonymized it with *C.* (*Macropodina*) *planatus*. Three related Nearctic Cremastocheilini were used as outgroups, namely *Genuchinus ineptus*, *Cyclidius acherontius* and *Cycl. elongatus*. *Genuchinus* is assumed to be a close relative based on overall morphological similarity (Alpert 1994) and other cremastocheilines are rare in collections. Alpert's key was used to identify numerous misidentified specimens, particularly species that appear to be part of larger species complexes (see Alpert 1994). A total of 52 adult external morphological characters were used in this analysis (see Appendix A). Inapplicable characters were coded as "-", while missing, unknown or highly variable characters were coded as "?" (see Appendix B for character coding used). The choice of characters was based in part on previous suggestions by Krikken (1982), who was the first to propose a set of characters only for *C.* (*Trinodia*). Characters related to genitalia and wing venation were not used because they have previously been established as invariant within the genus (Cazier 1938). Uninformative characters were removed from the analysis. Species that vary in relevant characters were coded as morphotypes of a spe-

cies to recognize this variability. Male and female characters were not coded separately as sexes are not known to differ in external morphology except for the presence of a tibial tooth in the males (Alpert 1994).

Initially, all characters were run equally weighted and non-additive. The final matrix included seven characters coded as additive (see Appendix A). The Parsimony Ratchet (Nixon 1999a) was implemented in NONA (Goloboff 1999), and run within Winclada (Nixon 1999b) with 50 iterations, beginning with one starting tree and weighting approximately 21% of characters (11/52). The trees obtained by the Ratchet were used as starting trees in a "max*" (TBR branch swapping) search that produced 24 equally parsimonious trees of 149 steps. Suboptimal trees were searched, but none were found, leaving 24 equally parsimonious trees of 149 steps. A more thorough search using mult*100 and a successive max* search algorithm was performed, but the same 24 equally parsimonious trees were found. A strict consensus of the optimal trees was performed, with 4 collapsed nodes, yielding a tree of 153 steps (CI = 0.46 and RI = 0.80, Fig. 1). Bremer support was determined using Nona, and was set to a support level of 5. Clade support was estimated using jackknifing where each search consisted of 1000 replications, 5 reiterations of random additions of taxa, and holding a maximum of 10000 trees per replication. TBR (max*) was initiated with one starting tree per replication.

Results

The strict consensus of 24 equally parsimonious trees (CI = 0.46, RI = 0.80) reveals several monophyletic, resolved clades. The genus *Cremastocheilus* is a well-defined, monophyletic group (Jackknife support = 97) comprised of several clades. The subgenera *C.* (*Macropodina*), *C.* (*Trinodia*), and *C.* (*Cremastocheilus*) are monophyletic. The *hirsutus* species group within *C.* (*Trinodia*) is well supported (Bremer support = 5; Jackknife support = 99). In contrast, *C.* (*Myrmecotonus*) is not a monophyletic group. The *armatus* and *crinitus* species groups within *C.* (*Myrmecotonus*) form a single monophyletic group, while the *schaumii* species group appears to be the sister group of the *Cremastocheilus sensu str.* + *Myrmecotonus* clade (including only *armatus* and *crinitus* groups). The recently described *C.* (*Myrmecotonus*) *tomentosus* Warner is closely related to the *crinitus* group, although it has been proposed as a sister to *C.* (*Myrmecotonus*) *robinsoni* (Warner 1985) in the *C. robinsoni* species group, which was not included in the analysis. Diagnosis of all equally parsimonious trees indicates that *C. wheeleri* [in (*C. Anatrinodia*)] is the sister of *C.* (*Cremastocheilus*). Overall, the trees found in this analysis agree with those of Krikken (1982), whereby *C.* (*Myrmecotonus*) and *C.* (*Cremastocheilus*) are closely related; however *C.* (*Anatrinodia*) is more closely connected with the *C.* (*Myrmecotonus*) + *C.* (*Cremastocheilus*) clade than with *C.* (*Trinodia*), which disagrees with original hypotheses (Casey 1915, Potts 1945) about a close relationship between *C.* (*Trinodia*) and *C.* (*Anatrinodia*).

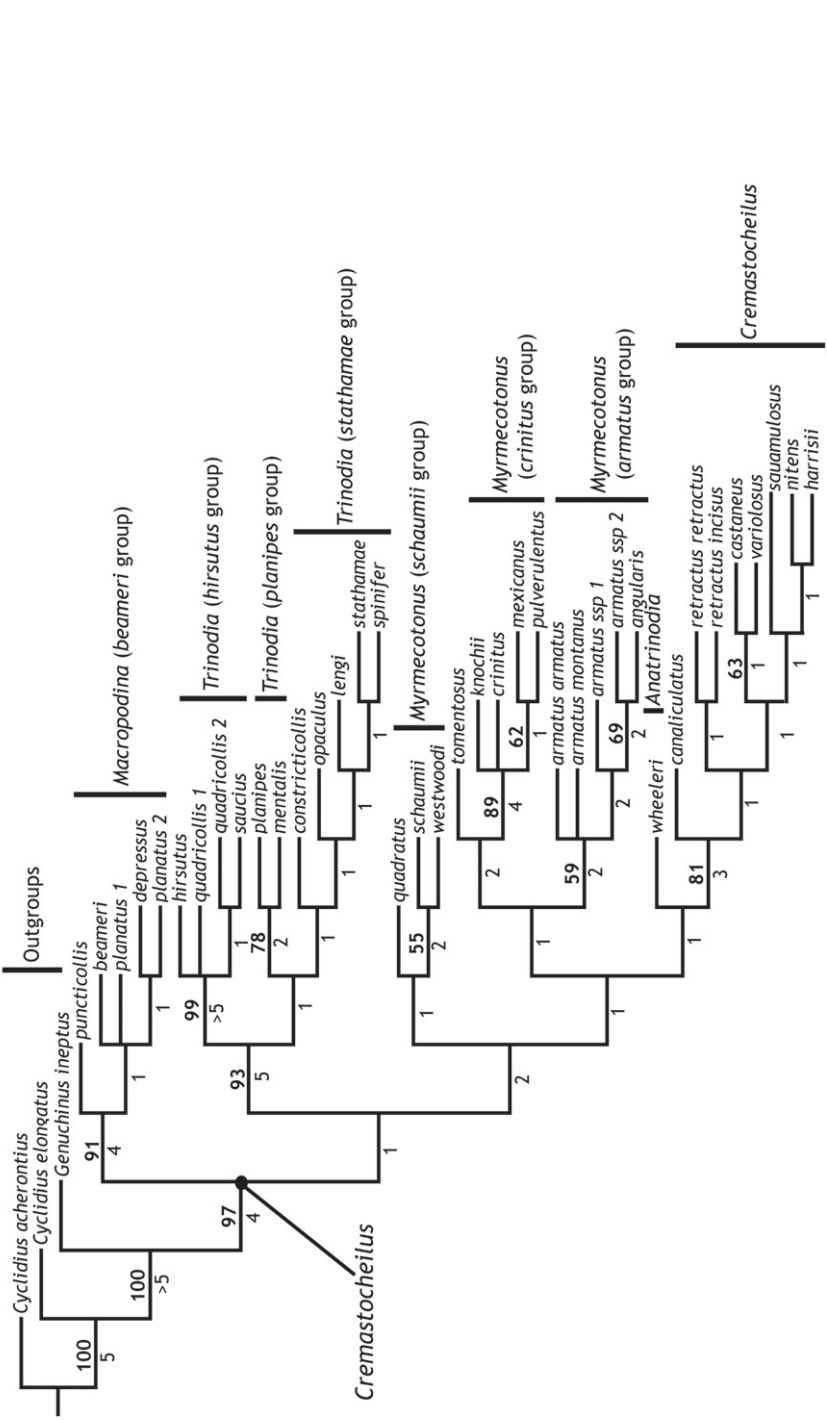

Figure 1. Strict consensus of 24 equally parsimonious trees (153 steps, CI = 0.46, RI = 0.80) of *Cremastocheilus*. Dark bars indicate monophyletic groups that correspond with Alpert's (1994) subgenera and respective species groups. Jackknife values are shown above branches, with support <50 not shown. Bremer support values are shown in bold below branches. Black dot indicates the genus *Cremastocheilus*.

Discussion

Based on all equally parsimonious trees found, the monophyly of the genus *Cremastocheilus* is well supported. Diagnostic characters include the presence of modified anterior and posterior pronotal angles and associated trichomes. Relationships within the genus support some previous hypotheses, but renders the validity of certain subgenera invalid. While subgenera *C.* (*Macropodina*), *C.* (*Trinodia*), and *C.* (*Cremastocheilus*) are monophyletic, *C. (Myrmecotonus*) is not. Similarly, the monotypic subgenus *C. (Anatrinodia*) is more closely related to *C. (Cremastocheilus*) than to *Trinodia,* with which it was previously united by similarity in pronotal shape.

Monophyly of *C.* (*Macropodina*) is supported by enlarged protarsi, frontolateral carinae bearing glands (Alpert 1994), carinate pygidium, and generally rectangular body shape. Within *C.* (*Macropodina*) there is poor support for species relationships below the subgeneric level, and Alpert also only suggested one species group, the *C.* (*Macropodina*) *beameri* group, which includes all species within this subgenus. There is little information regarding the hosts for this subgenus, although the species *C.* (*Macropodina*) *beameri* has been collected in and near rodent burrows. Cazier and Mortenson (1965) suggested that *C. beameri* uses rodent burrows, particularly those of *Neotoma* as sites for mating and overwintering for adults, as well as development of immature beetles. Ant colonies are often found within or near rodent mounds, and it is possible that these colonies are a source of brood for adults, although beetles have not been found in surrounding ant mounds in the field (Alpert 1994). The species *C.* (*Macropodina*) *planatus*, which is likely a widely distributed species complex, as well as its previously recognized synonym *C.* (*Macropodina*) *depressus* have been collected with *Camponotus* and there is no evidence that it is associated with rodent mounds. Similarly, *C. puncticollis* has been collected in *Myrmecocystus mexicanus* mounds, although this particular host record has been cited as accidental (see Alpert 1994 for host accounts for all species). While these beetles have never been observed to interact with ants, it has been suggested that the long forelegs can be used to wipe ants from the beetles' bodies while attempting to enter ant nests (Alpert 1994). Similarly, true functions of the frontolateral and protarsal glands are unknown, although they probably function together since the glands are identical in structure (Alpert 1994).

The monophyletic subgenus *C.* (*Trinodia*) is united by several unique synapomorphies that make it one of the most distinctive subgenera in the genus. All species bear a very prominent trilobed pronotum, a character that gave this subgenus its name. The presence of an upcurved proepisternum, which appears dorsally as a separate nodular lobe, is unique in this subgenus. Although a few unrelated species appear to have a slight frontoclypeal ridge, it is highly developed in *C.* (*Trinodia*). It is suspected that many of these characters are related to myrmecophily. Alpert's (1994) three species groups are all monophyletic. The *C.* (*Trinodia*) *hirsutus* group is a unique and well supported species group, with all species bearing an emarginate posterior pronotal angle. All species within this species group are found with ants in the genus *Pogonomyrmex*. It is likely that the robust and excised posterior angles in this species group is involved

in their interaction with these aggressive ant hosts. Two species in the species group *C.* (*Trinodia*) *planipes* are united by very broadly flattened hind tibiae and femora. Both *C.* (*Trinodia*) *planipes* and *C.* (*Trinodia*) *mentalis* are found with the ant genus *Aphaenogaster*. The *C.* (*Trinodia*) *stathamae* group is supported by unique elytral punctures that appear elongate and fused. This is the only monophyletic group that is united by a character related to punctation, as it appears highly homoplastic throughout the genus. Species in this group are collected with various species of the honeypot ants, *Myrmecocystus*, as well as *Pheidole*.

Species in *C.* (*Cremastocheilus*) comprise a monophyletic group and are united by several unique synapomorphies, including strongly delimited posterior angles and nodulose anterior angles. All species in *C.* (*Cremastocheilus*) bear a notched mentum of various sizes, except for *C. nitens* and *C. chapini*, although the monophyly of the subgenus is still preserved given the pronotal characters. In contrast, all species groups within *C.* (*Cremastocheilus*) suggested by Alpert (1994) are paraphyletic. His division of species groups relied mainly on characters related to shape of angles on the pronotum, shape of mentum, and elytral punctures; however, many characters related to elytral punctation show high incidences of homoplasy. The *C.* (*Cremastocheilus*) *canaliculatus* group is often defined by the presence of a secondary trichomes situated by the anterior pronotal angles; however, this character does not seem to be useful in defining the group.

The subgenus *C.* (*Myrmecotonus*) is not monophyletic, without removal of the *C.* (*Myrmecotonus*) *schaumii* group. This species group lacks highly developed pronotal angles as well as a notch in the proepisternum that is present in all other *C.* (*Myrmecotonus*). The analysis indicates that the *C.* (*Myrmecotonus*) *schaumii* group is the sister group to the *C.* (*Cremastocheilus*) + *C.* (*Myrmecotonus*) clade (with removal of the *schaumii* species group). Given that the host records indicate that a western United States distribution for all *C.* (*Myrmecotonus*) species, it is possible that specific ant hosts play an important role in the relationships indicated. The close relationship of *C.* (*Cremastocheilus*) and *C.* (*Myrmecotonus*) with removal of the *C. schaumii* group could be explained by similar ant hosts. With exception of a few other ant host genera, including *Aphaenogaster* and other accidental records (see Alpert 1994), all species in *C.* (*Cremastocheilus*) and the *C.* (*Myrmecotonus*) *crinitus*, *C.* (*Myrmecotonus*) *armatus*, and *C.* (*Myrmecotonus*) *robinsoni* species groups, are found with *Formica* ant hosts. Species in the *C.* (*Myrmecotonus*) *schaumii* group have only been collected with *Messor* species and was accidentally recorded with *Pogonomyrmex subnitidus* (Alpert 1994).

The relationship of the species *C.* (*Anatrinodia*) *wheeleri* with other species and subgenera has never been well understood due to its odd mentum and pronotal structures. Its initial union with *Trinodia* was based on elements of the pronotum. Unlike the tri-lobed pronotum, with the lateral lobes holding large muscles in *Trinodia*, the pronotum in *C. wheeleri* contains enlarged glandular clusters (Alpert 1994). The distinctly trilobed pronotum, up-curved proepisternum, and carinate clypeus support the monophyly of *C.* (*Trinodia*), characteristics that are not found in *C. wheeleri*. The strict consensus indicates that *C. wheeleri* is be a basal species of *C.* (*Cremastocheilus*), but

some have suggested that it is a highly derived relative of the subgenus (Warner, pers. comm.). The deeply cup-shaped mentum and notched proepisternum places it close to other *C.* (*Cremastocheilus*), but overall body shape does not match character definitions of any other subgenus. We are hereby synonymizing *C.* (*Myrmecotonus*) and *C.* (*Anatrinodia*) with *C.* (*Cremastocheilus*). Note that taxonomic perspective regarding species and subgenera should be cited as Mynhardt 2009 (in Mynhardt and Wenzel 2010).

The role of glands and associated trichomes and tomenta in beetle/ant interactions are not well understood and thus not described herein (but see Alpert 1994 for extensive histological study). Low consistency index (CI) values indicate a high occurrence of homoplasy, which could be due to myrmecophilous habits. Some behavioral work has shown that even species that are closely related do not interact with ant hosts in the same way. For example, *C.* (*Trinodia*) *hirsutus* enters nests on its own, without aid from ants, while closely related *C.* (*Trinodia*) *saucius* is pulled into mounds by ants (Alpert 1994). This could suggest that characters related to certain myrmecophilous behaviors are homoplastic. It might also suggest a divergence in behaviors that could lead to speciation. Ants are known to "lick" or bite pronotal angles of *Cremastocheilus*, which is likely to be rather host-specific with respect to the mandibles of the ants and may drive the evolution of the pronotal projections. Wheeler (1908) suggested that the shape of the posterior pronotal angles is likely shaped by ant mandibles. As such, the only pronotal characters that indicate relatively low CI values are the shape of the posterior angles (Wheeler 1908) and the appearance of a notch in the anterior pronotal angle in unrelated species of *C.* (*Trinodia*) and *C.* (*Cremastocheilus*). Ant hosts of these two groups differ, suggesting separate selective pressures by different ant hosts. Characters related to the patches of setae (tomenta) distributed across the body are also supported by low CI's. The frontoclypeal tomentum, elytral disk tomentum, and ventral abdominal tomentum appear in various unrelated *Cremastocheilus* species. Similarly, there is a strip of tomentum along the base of the mesepimeron, which is found in five species, only two of which are closely related. These tomenta are probably linked to interactions with ants, and may have associated exocrine glands. For example, the frontal tomentum is has been shown to be associated with the frontal glands found in histological sections in *C. wheeleri* and the *hirsutus* group of *C.* (*Trinodia*) (Alpert 1994). The placement of glands, which were coded by using external trichomes or tomenta, appears to be a relatively good character in distinguishing subgenera or even species groups, particularly in the case of trichomes. For example, tarsal glands are found only in *C.* (*Macropodina*) and frontal glands are found in closely related *C. wheeleri* and species in *C.* (*Cremastocheilus*). Externally, tomenta above the antennal insertions are associated with the frontal glands in *C.* (*Cremastocheilus*). Most species in the genus bear tomenta on the metepimeron and many species have tomentose areas along or on the lateral portion of the abdominal sterna. Alpert (1994) found evidence of glands in *C.* (*Trinodia*), *C.* (*Myrmecotonus*) *armatus* and *C.* (*Myrmecotonus*) *pulverulentus*. Other tomentose areas are not at all associated with internal glands, especially those tomenta on the elytra of many species, which appears to be highly homoplastic. Tomentum at the base of the mesepimeron in several species is also homoplastic. Similar tomenta are

found throughout the Cetoniinae. Alpert (1994) suggested that the elytral punctures were reliable in defining species groups and even identifying species in many cases. Elytral characters used in this analysis did not prove to be useful in uniting species groups, and three of the four elytral characters used had very low CI values. However, because most of Alpert's species groups appear to be well-defined, monophyletic clades, it is evident that many other useful characters still unite those groups.

While tomenta and other myrmecophilous structures may be under strong selective pressures by ants, it is also likely that distinct monophyletic groups revealed in this analysis are associated with specific ant host genera, a pattern that has been shown in sceptobiine staphylinids associated with ants (Danoff-Burg 1994). Alpert's (1994) *hirsutus* group in *C.* (*Trinodia*) is almost exclusively collected with *Pogonomyrmex* ant hosts; the *C.* (*Trinodia*) *planipes* group is associated only with *Aphaenogaster spp*; and *C.* (*Cremastocheilus*) species as well as *C. wheeleri* and the majority of species in *C.* (*Myrmecotonus*) are most often collected in *Formica* mounds. A few exceptions to this pattern includes *C.* (*Anatrinodia*) wheeleri, which is most often collected in *F. obscuripes* mounds. The unrelated *C.* (*Myrmecotonus*) is also most often found with this particular species; however, there is an indication that closely related *Cremastocheilus* species are more likely to be found with ant hosts of the same genus.

Conclusion

True interactions between beetles and their respective ant hosts should elucidate evolutionary patterns regarding strategies used by different *Cremastocheilus* species. Based on the characters used in this study, it is evident that many characters related to myrmecophily are informative at the subgeneric level, but others are not. Trichomes, which are assumed to play an integral part in beetle/ant host interactions, show low instances of homoplasy, while some tomenta and the elytral punctures indicate multiple origins and are less phylogenetically informative. This work presents a framework for future studies, but also presents some important taxonomic changes regarding subgenera. We suggest that any future work should include characters related to myrmecophilous habits, and addition of molecular data would be very useful.

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Appendix A.

List of the characters and character states used in the analysis. doi:10.3897/zookeys.34.262.app.1.ds.

Note: Consistency index (CI) and retention index (RI) resulting from analysis are indicated in parentheses. Characters are numbered beginning with "0". File format: PDF.

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Appendix B.

Morphological character matrix of analyzed species of *Cremastocheilus*, with states used for each character. doi:10.3897/zookeys.34.262.app.2.ds.

Note: States are numbered beginning at "0". File format: PDF.

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